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Proceedings of the Royal Society B.

DOI:
10.1098/rspb.2016.1716

Published: 23/11/2016

Peer reviewed version

PROCEEDINGS B

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Journal:	*Proceedings B*
Manuscript ID	RSPB-2016-1716.R1
Article Type:	Research
Date Submitted by the Author:	24-Oct-2016
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Subject:	Ecology < BIOLOGY
Keywords:	fish biomass, functional group, herbivore, human drivers, natural drivers, Pacific Ocean
Proceedings B category:	Population and community Ecology

Natural bounds on herbivorous coral reef fishes

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Abstract

Humans are an increasingly dominant driver of Earth's biological communities, but differentiating human impacts from natural drivers of ecosystem state is crucial. Herbivorous fish play a key role in maintaining coral dominance on coral reefs, and are widely affected by human activities, principally fishing. We assess the relative importance of human and biophysical (habitat and oceanographic) drivers on the biomass of five herbivorous functional groups among 33 islands in the central and western Pacific Ocean. Human impacts were clear for some, but not all, herbivore groups. Biomass of browsers, large excavators and of all herbivores combined declined rapidly with increasing human population density, whereas grazers, scrapers and detritivores displayed no relationship. Sea-surface temperature had significant but opposing effects on the biomass of detritivores (positive) and browsers (negative). Similarly, the biomass of scrapers, grazers and detritivores correlated with habitat structural complexity, however relationships were group-specific. Finally, the biomass of browsers and large excavators was related to island geo-morphology, both peaking on low-lying islands and atolls. The substantial variability in herbivore populations explained by natural biophysical drivers highlights the need for locally-appropriate management targets on coral reefs.

Keywords: fish biomass; functional group; herbivore; human drivers; natural drivers, Pacific Ocean

Introduction

Humans are increasingly a dominant global force influencing the structure and function of ecosystems through the removal of key species and functional groups, habitat modification, and the effects of pollution and climate change [1–3]. Coral reef ecosystems are especially vulnerable to such human-forcing [4], and while anthropogenic impacts are globally pervasive, they occur against a backdrop of high natural variability in reef systems caused by differences in the environment and bio-geographic context. Oceanic productivity, water temperature, habitat area, reef geomorphology and larval connectivity can have substantial impacts on coral reef fish assemblages [5–10]. For example, the natural fish carrying capacity of a coral reef has been shown to double along a gradient of increasing oceanic productivity [11]. Understanding the relative influence of human versus natural drivers is key to assessing the current status of these ecosystems.

Here we focus on one component of coral reef systems, namely herbivorous fishes in the Pacific Ocean. Despite some uncertainty, particularly in the Indo-Pacific, about the relative importance of herbivory in mediating coral-algal dynamics [12–16], herbivorous fishes are widely recognised to play an important role in maintaining the competitive dominance of reef calcifiers (e.g. hard corals and crustose coralline algae), over other benthic components (e.g. fleshy macroalgae) [17–20]. For example, following climate-induced coral bleaching, fished reefs with reduced herbivore populations have a greater propensity to become dominated by macroalgae [21]. For that reason, some coral reef management strategies now focus specifically on protecting or restoring herbivorous fish populations [22,23]. There is a need, therefore, to better understand the role of the natural environment in determining distribution patterns of herbivorous fishes [8,24–26] independent of local human impacts on coral reefs. Indeed, the upper bounds of herbivore biomass will be determined by a reef's local biophysical setting, and once identified, will allow for realistic fisheries management strategies to address the widespread effect of fishing on this trophic group [7,8,11,27–30].

Herbivorous reef fish assemblages vary with local environmental factors. For instance, parrotfish tend to be more abundant and species-rich on barrier reefs compared to atoll, fringing or low coral cover reefs [31]. Intra-island variation in herbivore species composition and behavior is also evident among different reef habitats. Typically, the abundance and feeding activity of grazing surgeonfishes and large parrotfishes is lower on near-shore coastal reefs compared to wave exposed offshore reefs [32,33]. Conversely, browsing herbivores are often more abundant on wave protected back reef habitats, as compared to exposed fore-reef areas [32,34,35]. Furthermore, herbivore biomass and rates of herbivory tend to be greatest on the reef crest, and both decrease across the reef flat and down the reef slope [35–38]. These patterns in herbivorous fishes are variously attributed to the availability and quality of food and shelter, in addition to the wave energy, and sedimentation regimes experienced [34,38–40]. The implication of this localised among- and within-habitat variation is that the need

for, and potential effectiveness of, fishery management interventions are highly dependent on natural bounds set by the location's biophysical setting [41].

Here we make use of a consistent monitoring dataset from 33 islands and atolls across the central and western Pacific to better understand the relative role of anthropogenic impacts and biophysical drivers (habitat and physical environmental conditions) in structuring herbivore populations on coral reefs. These islands span large gradients of human population density (0-27 people per hectare of reef) [11,42] and biophysical condition [43], allowing us to separate the relative effect of those in driving variation in herbivore biomass.

Methods

Fish assemblage and reef habitat surveys

We used coral reef monitoring data collected between 2010 and 2015 across 33 Pacific islands and atolls (electronic supplementary material table S1). The surveys were performed for the National Oceanic and Atmospheric Administration (NOAA) Pacific Reef Assessment and Monitoring Program (Pacific RAMP), a long-term ecosystem monitoring effort focused on United States and United States-affiliated coral reefs [44]. Data from two underwater visual census techniques were used, the stationary point count (SPC) and the towed-diver (tow) survey method [45,46]. The SPC was used to estimate the biomass of herbivorous fishes, whilst the latter was used to estimate biomass of large (>50 cm in total length) piscivores. Piscivore biomass was used to investigate what effect, if any piscivores may have in exerting top-down control on herbivore populations [47]. The tow estimates of piscivore biomass was used in preference to the SPC due to the concern that small-scale surveys can overestimate the biomass of large roving predators, such as sharks and jacks [48].

A total of 3309 SPC surveys were conducted by experienced surveyors. Survey site locations were selected per sampling unit (typically an island / atoll, occasionally a cluster of small islands, or for large islands, island sub-section) by means of a randomised stratified design [49]. The target sampling domain of Pacific RAMP is hard bottom habitat in depths less than 30 m, and site allocation is stratified by reef-zone (fore-reef; back reef; lagoon) and depth (0-6 m; 6-18 m; 18-30 m). Only data from the fore-reef habitat were used to remove any biases associated with inter-habitat differences on herbivorous fish assemblages; the fore-reef is the most comparable reef habitat present across all islands. At each survey site, a pair of divers conducted simultaneous adjacent counts in which they first compiled lists of all fish species present within their survey area (7.5 m radius cylinder) during a 5-minute interval. After the timed interval, divers proceeded to count and size all fishes from the species list within their survey area. Divers then visually estimated benthic cover and reef complexity, the mean vertical substrate height from the reef plane in the survey cylinder.

A total of 861 tow surveys were analysed. Surveys were haphazardly located on reef areas at a depth of 10-20 m, with the broad goal of spreading sites as widely

as possible around each island; circumnavigating the island where practical. A pair of divers (one fish, one benthic surveyor) were towed behind a small boat travelling ~2 km for each 50-minute survey. During each tow, the fish diver recorded the number and size of all species > 50 cm in total length within a belt-transect extending 5 m on either side and 10 m in front of the diver, from the seafloor to the surface. Full details on the tow survey method are available in [48].

Data processing

The weight per individual fish was calculated using length-to-weight relationships from FishBase and other sources [50,51]. To date, much of the evidence of human impacts on herbivore populations relative to regional biophysical variation considers these herbivorous fishes as a single trophic guild or broad taxonomic groups [8], although see [24]. Collectively these studies point to differences in the expected richness and biomass of herbivorous fishes, either *in toto* or of specific families, based on habitat, island type, and biogeographic region [7,8]. There is, however, increasing evidence that different herbivore functional groups perform complimentary roles in reef processes [52], have different dietary and habitat requirements [8,53,54], and are likely to respond differently to local biophysical settings. Therefore, we classified herbivores functionally (*sensu* [55]) and incorporated new dietary data specific to the study area. Five groups resulted: 'browsers', 'grazers', 'detritivores', 'large excavators/bioeroders' and 'scrapers/small excavators' (electronic supplementary material S2).

For the SPC surveys, site-level herbivorous fish biomass (g m^{-2}), hard coral cover and reef complexity were calculated by averaging the two diver replicates conducted at each site location. Data were inspected for site-level outliers, site level observations of any of the fish metrics that were > 97.5% the inter-quartile range, were capped at that 97.5% value (electronic supplementary material S3). Island-scale averages of the site level metrics were calculated, first by averaging values within each depth stratum per island, and then weighting the mean estimates by the total area of each stratum per island [56,57]. Island-level tow estimates of piscivore biomass were calculated as equally weighted means of each tow per island across years. Species richness per functional group was estimated by generating species accumulation curves for each island using the rarefaction method in the R package *vegan* [58].

Quantifying human and biophysical predictors

We used published estimates of the following human and biophysical covariates, derived at the island level: human population density, chlorophyll-a (mg m^{-3}) as a proxy for phytoplankton biomass and oceanic productivity, total area of reef habitat, sea-surface temperature (SST °C), wave energy (kW m^{-1}) and island type (electronic supplementary material table S3.1). Island types were based on geomorphology, and classed as either high (e.g. basalt island) or low-lying (e.g. carbonate island or atoll). Islands were also grouped by region (Hawaii, Central

Polynesia, Gilbert, Ellis and Marshall Islands and Tropical Northwest Pacific [59]).

To determine anthropogenic impacts on herbivorous fishes, we used human population density (the number of people resident per island (from the 2010 US census) divided by the area of fore-reef habitat per island from GIS habitat layers maintained by Pacific RAMP (electronic supplementary material S3.1). For the remote-sensing data, we used the lower climatological mean of sea-surface temperature from the Pathfinder v5.0 dataset, and the climatological mean of chlorophyll-a derived from the Moderate Resolution Imaging Spectroradiometer (MODIS). The wave energy metric used was the climatological mean from NOAA's Wave Watch III wave model. Details on the methods used to generate island specific biophysical metrics are described in full in [43].

Modeling

We fitted generalised additive mixed-effects models (GAMM) of island-level herbivore biomass (electronic supplementary material S3) in R (ww.r-project.org), using the *gamm4* package [60]. All models included region as a random effect to account for autocorrelation amongst islands within regions [61]. Wake is the only replicate in the Marshall, Gilbert and Ellis Islands region, therefore we report summary fish metrics for Wake (biomass and richness) but excluded it from the statistical modeling (total number of island replicates = 33). For total fish biomass and functional group biomass separately, we fitted GAMMs for all possible combinations of the predictor variables using the *UGamm* wrapper function, in combination with the *dredge* function in the *MuMIn* package [62].

We calculated Akaike's Information Criterion, corrected for small sample size (AICc) and the AICc-based relative importance weights (w_i) to assess the conditional probability of each model. We report the model-average estimates for each predictor term based on the top-ranked models for each fish metric, top-ranked models being those with > 0.05 Akaike weight. To test for influential data points and to check for model stability, we performed a jack-knife sensitivity test, calculating the percentage of times sequentially deleting single response variable data points produced the same top-ranking model structure (*sensu* [63]). Finally, to visualise the effect of predictor terms on the herbivorous fish responses, we used the coefficients from the top-ranked models for each response variable separately to generate a predicted dataset. We set all other predictors terms to their median value then generated smoother terms for the predictor of interest and plotted these against the untransformed, un-scaled fish metrics [11].

Results

Across the western central Pacific, a large degree of variability exists in the biomass and composition of herbivorous fish assemblages, including the species richness within functional groups. Generally, there is greater biomass and richness of detritivores in Central Polynesia, and a greater biomass of browsers

in the unpopulated northerly latitudes (figure 1, electronic supplementary materials S4). Functional group biomass and richness was positively related in large excavators/bioeroders, scrapers/small excavators and detritivores (Figure S4, Table S4).

Major drivers of this spatial variation in total herbivorous fish biomass were identified as reef complexity, hard coral cover and human population density (electronic supplementary material table S5). The original smoothers fitted to the functional group and total herbivore biomass values are in electronic supplementary material figure S5. Total herbivore biomass plateaued at intermediate complexity, decreased at highest coral cover, and continually decreased with human population density (electronic supplementary material figure S5). The best-fit model that contained these three biological variables had high explanatory power and stability (~69% variability explained in total herbivore biomass, 94% jack-knife stability; electronic supplementary material table S5). When functional groups were modeled individually, the top candidate models showed similar stability. Specifically, the dominant predictors identified from the variable importance (vi) estimates from the top candidate model of the entire dataset matched those identified from the jack-knifing method (electronic supplementary material table S5). The amount of variance explained by the top-ranking models of herbivore biomass for each functional group (figure 2) was as follows: browsers (84%); detritivores (84%); grazers (73%); scrapers/small excavators (36%) and; large excavators/bioeroders (59%) (electronic supplementary material figure S5).

The relationship between the top predictor terms and herbivore biomass were distinct for different functional groups. Biomass of large excavators/bioeroders (all parrotfishes > 35 cm in total length) and browsers was significantly greater at low islands/atolls as compared to high islands (figure 3, electronic supplementary material table S5). These were also the only functional groups for which human population density was a strong predictor of biomass (figure 3, electronic supplementary material table S5), with both groups declining rapidly from low to mid human population density.

The dominant drivers of variability in browsers, detritivores and grazers and scrapers/small excavators were biophysical. These data showed that reefs in warmer waters have lower browser biomass and greater detritivore biomass and species richness (figure 3, electronic supplementary material table S5). Increased detritivore, grazer and scraper/small excavator biomass was evident from low to mid habitat complexity. The biomass of grazers continued to increase at high complexity locations, whereas for detritivores and scrapers/small excavators the biomass either plateaued or was reduced at high complexity (figure 3). Locations with a larger amount of fore-reef habitat had greater biomass of detritivores, while areas with intermediate wave-energy and high chlorophyll-a had increased grazer biomass (figure 3, electronic supplementary material table S5).

Discussion

Our results are consistent with the growing understanding that regional variability in the biophysical attributes of coral reef ecosystems acts to determine ecological state independent of local human impacts [11,63,64]. Specifically, our findings confirm clear anthropogenic impacts to herbivorous fishes across the Pacific, but importantly also show that; i) effects are functional-group specific and; ii) the biophysical attributes of reefs, especially sea-surface temperature (SST) and large-scale geo-morphological habitat complexity also drive herbivorous coral reef fish assemblage states. Prior to this study, quantitative evidence for anthropogenic impacts on herbivorous fishes, while simultaneously accounting for large-scale natural variability in fish assemblages, has been sparse [8,30,31]. To our knowledge, this is the first ocean basin-scale study quantifying the relative effects of human versus natural biophysical drivers of herbivorous fish functional group biomass.

In the absence of fisheries dependent data on subsistence, recreational and commercial take, human density and distance to market have proven to be useful proxies for the influence of humans on coral reef fishes [11,65,66]. Our results show a steep and rapid decline in the biomass of large excavators and browsers with increasing human population density. This pattern is consistent with other global and regional assessments documenting the negative effect of fishing on herbivores [27,28]. Herbivorous fishes, in particular large excavating parrotfishes, and browsing surgeonfishes, are highly desired fisheries targets in the Pacific [67–70]. Our results demonstrate the sensitivity of populations of these large herbivores to fishing mortality, presumably due to their large maximum body size and for some species, late age at maturity and the disproportion contribution of large old females to population replenishment [67,71–74]. The vulnerability of these two functional groups to human impacts is particularly important as they contribute disproportionately to reef processes [52,75,76].

Herbivores vary in richness, abundance and biomass by island geomorphology [8,31]. Our results show ~ 24-45% greater biomass of large-excavating and browsing fishes at low-lying islands (carbonate) and atolls, compared to high islands (basalt). There was no evidence for an island type effect for the remaining functional groups, although consistent with a previous study [8], we found that the biomass of detritivores (all acanthurids) was positively associated with reef area. It may be that this island type difference in biomass is driven by differential species-specific habitat requirements. For example, lagoonal habitat for settlement or nursery areas [77] is only present within atoll systems. The implications of our analyses are that large-scale habitat differences should be considered before comparing herbivorous fish assemblages across different island types.

Here we found no consistent relationship between the biomass of different herbivore functional groups and the cover of hard corals, but still an overall relationship between coral cover and total herbivore biomass. Our results suggest that in areas of coral cover greater than 22-24% the total herbivore assemblage will tend to be reduced in biomass, whilst the biomass of grazers, detritivores and scrapers/small excavators increases with habitat complexity,

with peak biomass for scrapers and detritivores at intermediate complexity. Previously, a non-linear association between coral species richness and fish community abundance has been shown [78], as has a reduction in abundances of small and medium sized herbivores at low habitat complexity [79]. Taking these effects of complexity and coral cover together it seems plausible that this reflects the opposing changes in the availability of refugia and food with coral cover. In general, high coral cover, and associated structural complexity, reduces the foraging efficiency of predators [79–81]. Furthermore, the availability of shelter reduces the energy that fishes must allocate to swimming in high flow water environments [34], giving them an energetic advantage. As such, more complex environments support higher fish abundances [82]. However, increases in coral cover are accompanied by concomitant decreases in cover of other benthic organisms, such as turf, endolithic, and macroalgae [83]. These algal assemblages, and associated detritus, are the primary food sources for herbivores, and as such food availability may limit population size in areas of high coral cover. This notion is supported by several studies that have documented increases in the abundance and biomass of herbivorous fishes following extensive coral mortality and reduced structural complexity [84–86].

The increased biomass of grazers in areas of moderate wave exposure and increased oceanic productivity could also be related to food availability. Both algal and detrital mass tends to decrease with increasing wave energy and the highest edible algal mass occurs at moderately exposed reefs [87]. The positive association between chlorophyll-a and grazer biomass could be due to greater food availability for grazing fishes, specifically nutrients and sinking detrital particles like phytodetritus, feces or dead planktonic material [79]. If this were the case, one might expect to see a similar effect on detritivore biomass, however, we did not. Instead, the dominant biophysical driver of variability in detritivore biomass was sea surface temperature (SST).

Notably, detritivores and browsers showed opposing responses to SST, with browser biomass being negatively and detritivore biomass positively related to SST. Similar decreases in the biomass of browsing fishes with decreasing latitude, and hence SST, are evident in both the Atlantic [25] and southern Pacific Ocean [88]. Temperature fundamentally constrains the metabolic processes of ectotherms and various hypotheses have been proposed to explain how temperature might impact the performance and fitness of individuals [89]. For instance, the temperature-size rule predicts ectotherms to be smaller in warmer waters, due to reduced mean body size, earlier maturation and increased initial growth rates [90–92]. While the temperature-constraint hypothesis relates to the interacting effects of temperature and food quality on fish physiology [25,93]. Here we found increased browser biomass in cooler waters and increased detritivore biomass in warmer waters. Whether these trends in the standing stock of these functional groups relates to larger individuals and/or intra-specific variability in life history characteristics across the temperature gradients surveyed would require location specific age-based studies on individual species.

The different effect of temperature on these functional groups could also be a response to the very different dietary strategies of these fishes. Browsing acanthurids, such as *Naso unicornis,* and kyphosids, are the only functional group that hindgut ferment, which allows these fish to gain energy from refractory fleshy macroalgal carbohydrates, including mannitol [94–97]. Macroalgae, the preferred food of browsers is more abundant on reefs in cooler climes in the Pacific [63] and thus browser biomass may be tracking the availability of their target resource. It is difficult to ascertain the primary nutrient sources of detritivores which feed on the epilithic algal matrix (EAM) [98]. The EAM contains a mixture of filamentous algal turfs, cyanobacteria, macroalgal spores, microalgae (diatoms and dinoflagelletes), heterotrophic bacteria, sediment and organic detritus [99]. Stomach content analyses of the detritivore *Ctenochaetus striatus* reveal large amounts of loose plant cells, sediment and algal filaments while the composition of short-chain fatty acids in *Ctenochaetus striatus* and *Ctenochaetus strigosus* guts are indicative of a diet of diatoms and bacteria [53,100]. Whether detritivorous fish biomass tracks spatial variability in the abundance and production of their target resource remains to be established.

Conclusions

Our findings highlight that coral reefs' biophysical setting strongly determine their carrying capacity and community composition of herbivorous reef fishes. Human impacts are superimposed over the back-drop of these naturally occurring drivers. Herbivore-focused management interventions are likely to become more widely implemented due to the perception that greater herbivore biomass promotes reef resilience. Our results show large natural differences in the capacity of individual reefs to support herbivore populations and therefore it is unlikely that all reefs will respond similarly to particular interventions, such as prohibition of fishing. Moreover, our results show that herbivore functional groups respond in different ways along gradients of those natural biophysical drivers. Locally-appropriate management targets for herbivore functional group biomass must therefore factor in the natural bounds set by the reef's biophysical setting.

Data accessibility

All raw data collected for the Pacific Reef Assessment and Monitoring Program are available upon request (email: nmfs.pic.credinfo@noaa.gov). All data used within the paper are available at: https://github.com/fish-crep/canned-fish

Author contributions

AH, IDW and ASH conceived and designed the analysis; AH and GJW performed the analysis; all authors wrote the paper.

Funding

Data collection was funded by NOAA's Coral Reef Conservation Program (CRCP) (http://coralreef.noaa. gov). The research was funded by a CRCP grant (828) (AH).

Competing interests

We have no competing interests.

Acknowledgements

We thank Rusty Brainard for leading the Coral Reef Ecosystem Program and the extraordinary work of those involved in Pacific RAMP, Melanie Abecassis for statistical advice, Amanda Dillon for assistance with graphics, James Robinson for providing distance to provincial capital data, and Brett Taylor for helpful discussion and comments on an earlier version of this manuscript. We would also like to thank the four anonymous reviewers, whose thoughtful critique greatly improved this paper.

441 **Figure captions**
442
443 **Figure 1. Herbivorous fish biomass by functional group per region**. B =
444 browsers (red), D = Detritivores (green), G = Grazers (yellow), S = scrapers and
445 small excavators (blue), E = Large excavators and bioeroders (dark blue).
446 Trop.NW.Pacific = Tropical Northwest Pacific, C. Polynesia = Central Polynesia,
447 M. = Marshall Islands. AGS = Alamagan, Guguan and Sarigan, FDP = Farallon de
448 Pajaros, O&O = Ofu and Olosega, FFS = French Frigate Shoals, P&H = Pearl and
449 Hermes. Islands within region are ordered by Latitude.
450
451 **Figure 2: Model performance of generalised additive mixed effects models**
452 (GAMMs). T = total herbivores (grey), for remaining letter and colour codes see
453 figure 1. Rows represent separate model fits, colored bars indicate that the
454 predictor was included in a particular model and the height of each row adjusted
455 to the cumulative Akaike weight, expressed as a proportion of all fitted models. I
456 = model intercept term, ISL.TYPE = island type, CHL = chlorophyll-a, COMP = reef
457 complexity, CORAL = hard coral cover, HUM = human population density, PISC. =
458 piscivore biomass, TEMP = sea surface temperature, AREA = area of habitat,
459 WAVES = wave energy.
460
461 **Figure 3: Predicted biomass and 95% confidence limits of functional**
462 **groups by island type and along human and biophysical gradients:** human
463 population density; sea surface temperature, habitat complexity; wave energy,
464 area of fore-reef and chlorophyll-a. Functional groups are indicated by color code
465 and letter (see figure 1).
466

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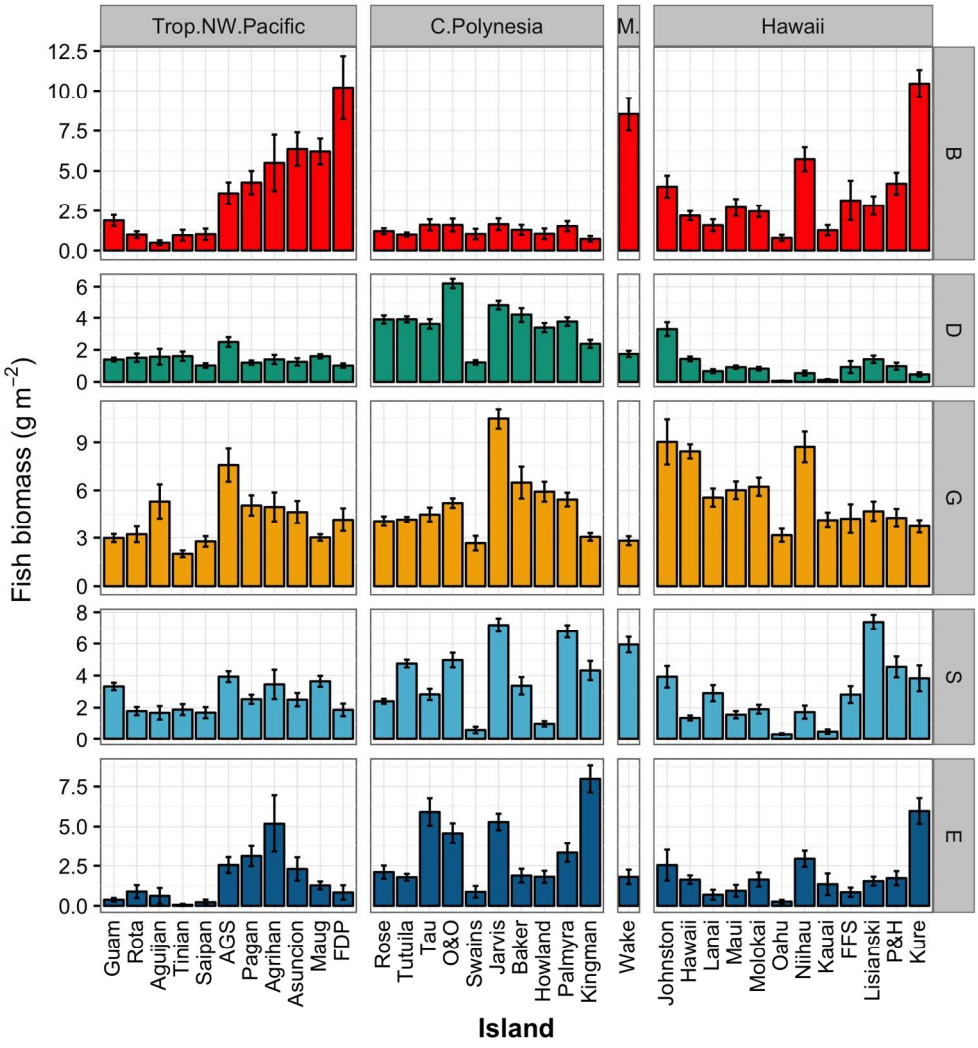

Herbivorous fish biomass by functional group per region. B = browsers (red), D = Detritivores (green), G = Grazers (yellow), S = scrapers and small excavators (blue), E = Large excavators and bioeroders (dark blue). Trop.NW.Pacific = Tropical Northwest Pacific, C. Polynesia = Central Polynesia, M. = Marshall Islands. AGS = Alamagan, Guguan and Sarigan, FDP = Farallon de Pajaros, O&O = Ofu and Olosega, FFS = French Frigate Shoals, P&H = Pearl and Hermes. Islands within region are ordered by Latitude.

figure 1

666x708mm (72 x 72 DPI)